American Fern Journal 91(4):187–196 (2001)

Vernal Photosynthesis and Nutrient Retranslocation in *Dryopteris intermedia*

JACK T. TESSIER
State University of New York, College of Environmental Science and Forestry, 350 Illick Hall, 1 Forestry Drive, Syracuse, N.Y. 13210 jttessie@syr.edu

ABSTRACT.—The value of preserving wintergreen fronds into the spring by forest understory fern species is unknown. In this study, net photosynthetic rates and nitrogen and phosphorus contents were monitored in a population of *Dryopteris intermedia* throughout a spring season to explore potential photosynthetic and retranslocational benefits of wintergreen fronds. Net photosynthesis occurred throughout the study indicating a potential for movement of fixed carbon from wintergreen fronds to other parts of the plant. Nitrogen and phosphorus content in the old fronds did not change through spring, thus no evidence for net retranslocation of these nutrients from wintergreen fronds to the rest of the plant was obtained. Maintenance of the wintergreen fronds may simply increase retention time and thus nutrient use efficiency of limiting nutrients. Other possible benefits of wintergreen fronds exist and should be investigated.

INTRODUCTION

The herbaceous understory layer of northern hardwood forests exhibits a plethora of leaf phenologies (Mahall and Bormann, 1978). One group of ecological importance is the wintergreen ferns. Species of this group maintain their fronds through winter and into spring only senescing after the current year's fronds begin unfolding. This contrasts with evergreen ferns, which maintain a set of fronds for more than one year. The value of over-winter maintenance of fronds has been hypothesized for some time (Monk, 1966; Chabot and Hicks, 1982; Moore, 1984; Van Buskirk and Edwards, 1995), yet tests of these hypotheses are limited (but see Minoletti and Boerner, 1993).

If the old fronds of *Dryopteris intermedia* (Muhl.) A. Gray are removed, the new fronds have a slower growth rate and begin to unfold later than if the old fronds are left intact (Van Buskirk and Edwards, 1995). Van Buskirk and Edwards (1995) hypothesized, in accordance with Moore (1984), that the old fronds either provided a photosynthetic or nutrient storage source to the plant that promoted the growth of the new fronds. Chabot and Hicks (1982), in reviewing the topic, also supported the view that wintergreen fronds provide a source of assimilation. The actual importance of the old fronds in this species has not been quantified.

The wintergreen fern *Polystichum acrostichoides* (Michx.) Schott is capable of year-round photosynthesis and nutrients are retranslocated from senescing old fronds back to the plant (Minoletti and Boerner, 1993). Also, the evergreen fern *Polypodium virginianum* L. was found to have photosynthetic peaks in the spring as a result of cool temperatures and high humidity, permitting more efficient CO_2 uptake (Gildner and Larson, 1992). Increased availability of soil nitrogen in spring (Murdoch and Stoddard, 1992, 1993; Zhang and Mitchell, 1995; Creed *et al.*, 1996; Mitchell *et al.*, 1996) may also help to increase photosynthetic rates (Chapin, 1980; Field and Mooney, 1986; Evans, 1989). These phenomena may be important for *Dryopteris intermedia*, making it energetically beneficial for this species to maintain photosynthetic tissues through spring. Likewise, retranslocation of nutrients from senescing organs, as shown in other herbs (DeMars and Boerner, 1997), can be of adaptive advantage by increasing the nutrient use efficiency of limiting nutrients (Chapin, 1980). Also, merely retaining old fronds for a longer period of time may increase nutrient use efficiency (Escudero et al., 1992). Thus, old fronds of *Dryopteris intermedia* may increase nutrient use efficiency through retranslocation of limiting nutrients or by extending the time over which a captured nutrient resource is used.

This study was designed to assess the photosynthetic and retranslocative benefits of wintergreen fronds in *Dryopteris intermedia*. The first objective was to measure net photosynthetic rates in old fronds through spring to determine if they are capable of photosynthesizing and therefore have the potential to provide a vernal fixed carbon source to the plant. The second objective was to measure nitrogen and phosphorus pool sizes through spring within component parts of *Dryopteris intermedia* and note changes in nutrient allocation that would indicate potential retranslocation.

METHODS

A second growth northern hardwood forest was selected in the Catskill Mountains, NewYork, in which *Dryopteris intermedia* was abundant. Within each of twenty randomly located one-square-meter plots, a single wintergreen frond was randomly selected for study. Net photosynthetic measurements were made using an LCA-3 Carbon Dioxide Leaf Chamber Analysis System (Analytical Development Co., Ltd., 1988) between 10 AM and 2 PM on clear days. Air flow during measurements was 185 mL / minute. Ambient light levels, temperatures, and relative humidities were used in order to get an accurate reflection of the field net photosynthetic rates during spring. Measurement commenced as soon as the ground was free of snow (April 3, 1999) and was repeated through frond senescence (May 29, 1999). A total of three estimates of net photosynthetic rate in each of the twenty fronds were made through the spring. Also, cover and density of *Dryopteris intermedia* fronds were measured at bi-weekly intervals in these permanent plots from April 3 until May 29, 1999.

A plot of mean cover and density versus sample size indicated that at least 15 sample plots were necessary to accurately reflect the overall cover and density of *Dryopteris intermedia* within the stand. It would, however, have been logistically unfeasible and ecologically damaging to harvest so many plots at each study interval. Therefore, six additional randomly located sample plots were studied and harvested at each biweekly interval. In these plots, *Dryopteris intermedia* cover and frond density were measured and then all biomass was carefully harvested, placed in plastic bags, and stored in coolers for transport to the lab. Roots and rhizomes were harvested by hand after scoring the perimeter of the plot with a shovel and carefully unearthing the root mat to collect the entirety of the fern belowground structures. Latex gloves were worn during harvest and subsequent handling in the lab to prevent contamination.

In the lab, the plant tissue samples were cleaned of soil using distilled, deionized water and placed in paper bags then dried at 60°C. Samples were separated into old fronds, belowground tissue, and (in the last two harvests) new fronds. The new fronds were not separated from the belowground tissue during the study until they had begun to unfurl. Next the samples were weighed and ground using a Wiley Mill to pass through a 1mm screen. These samples were then analyzed for N by Kjeldahl digestion (Bickelhaupt and White 1982). Lastly they were subjected to microwave digestion with nitric acid using a CEM MDS 81D (Gilman, 1988) and analyzed for P using a Perkin-Elmer Optima 3300 DV ICP.

Fern component specific regressions for biomass on a meter square of land area basis were determined for the 6 harvest plots based on cover and density of fronds at each sample date. Using this regression it was possible to estimate biomass in the 20 permanent plots thereby providing a more accurate estimate of stand level biomass than would be given by the six harvest plots, alone. Multiplying N and P concentration (from the analytical procedures) by biomass per fern component (from the regressions) permitted an estimate of N and P content on a meter square basis. Standard errors of these combined estimates were determined using equations from Avery and Burkhart (1994).

All statistical analyses were performed using SAS version 6.12 (SAS Institute, Inc., 1997). Differences in net photosynthetic rate among the three estimates were found using ANOVA followed by a Tukey's Honestly Significant Difference Test ($\alpha = 0.05$). Differences in N concentration and content, P concentration and content, and biomass among the fern components and harvest times were isolated by ANOVA followed by a Tukey's Honestly Significant Difference Test ($\alpha = 0.05$).

RESULTS

Wintergreen fronds were capable of positive net photosynthesis throughout the spring season (Figure 1). The highest rate of net photosynthesis was observed early in spring immediately after snowmelt. Remarkably, positive net photosynthesis was evident even in later stages of senescence (browned and withering) toward the end of the study.

Nitrogen content in the wintergreen and new fronds exhibited no change during the spring season (Figure 2a). Nitrogen values for belowground structures, on the other hand, first increased and subsequently decreased (Figure 2a). These belowground structures contained the majority of the N in the plants, particularly early on.

The nitrogen concentration of the different plant components did not change significantly through spring (Figure 2b). As the new fronds were not yet fully

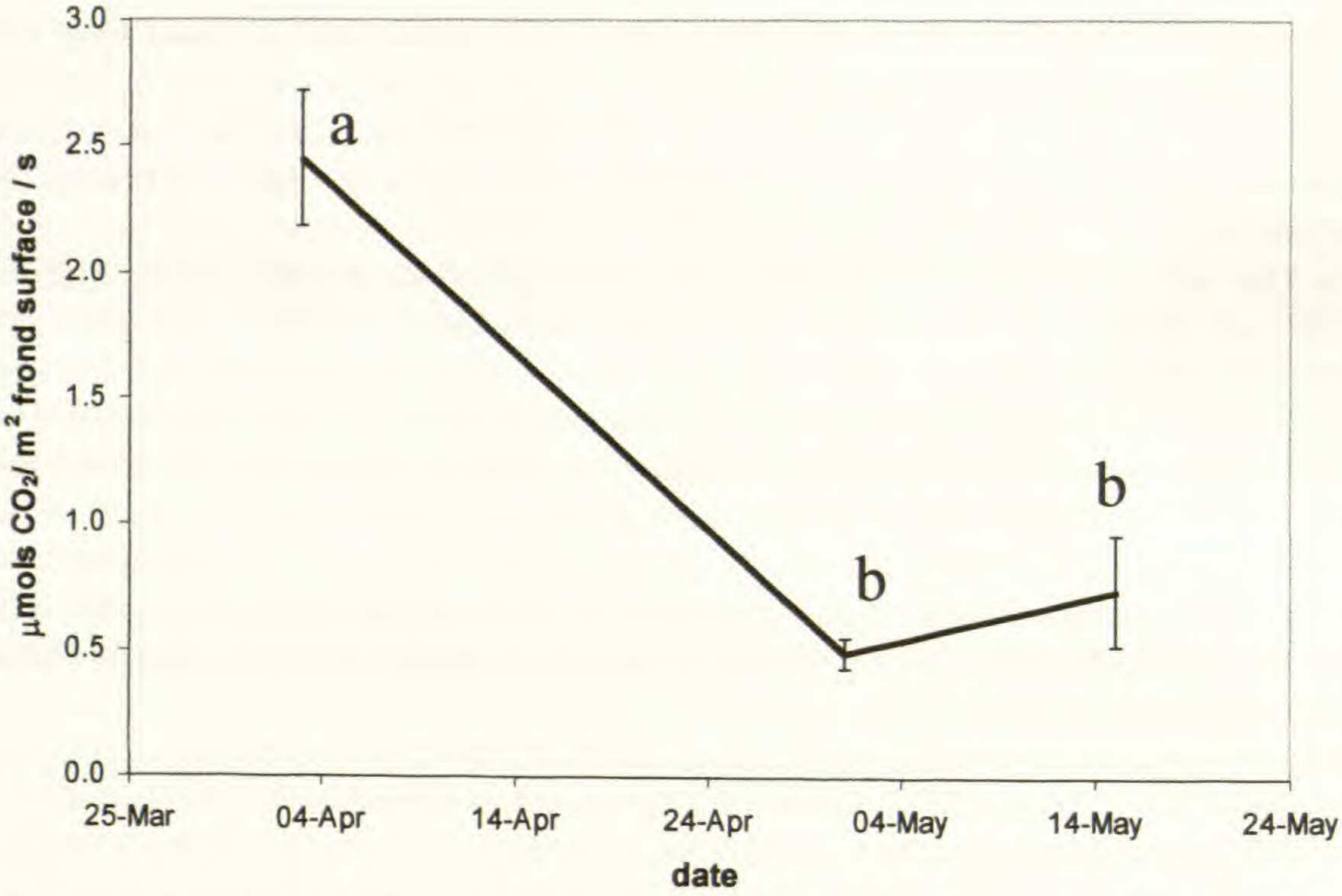


FIG. 1. Net photosynthesis through spring. Means with the same letter were not significantly different at $\alpha = 0.05$. Error bars indicate one standard error above and below the mean.

expanded at the end of the study, their N concentration was markedly higher than that of the other fern components. Figure 2c shows biomass of the fern components through time. Although the variations in biomass through time were not statistically significant, they do follow the pattern seen for N and P content (see below).

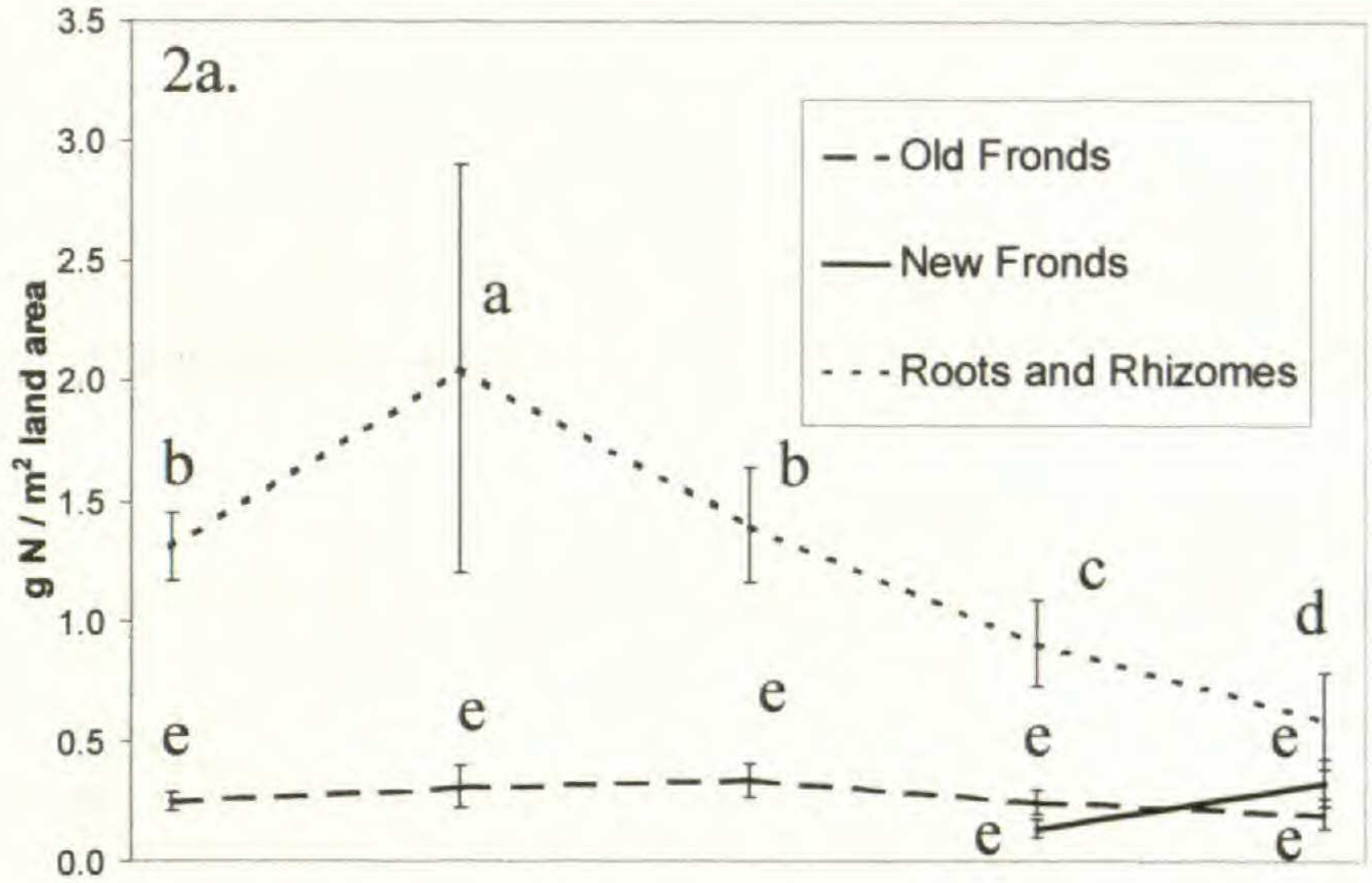
The trend in phosphorus content (Figure 3a) was similar to that for nitrogen. Wintergreen and new fronds remained constant in their P content while belowground structures increased and then decreased with time. The phosphorus concentration trend (Figure 3b) was very similar to that of N concentration.

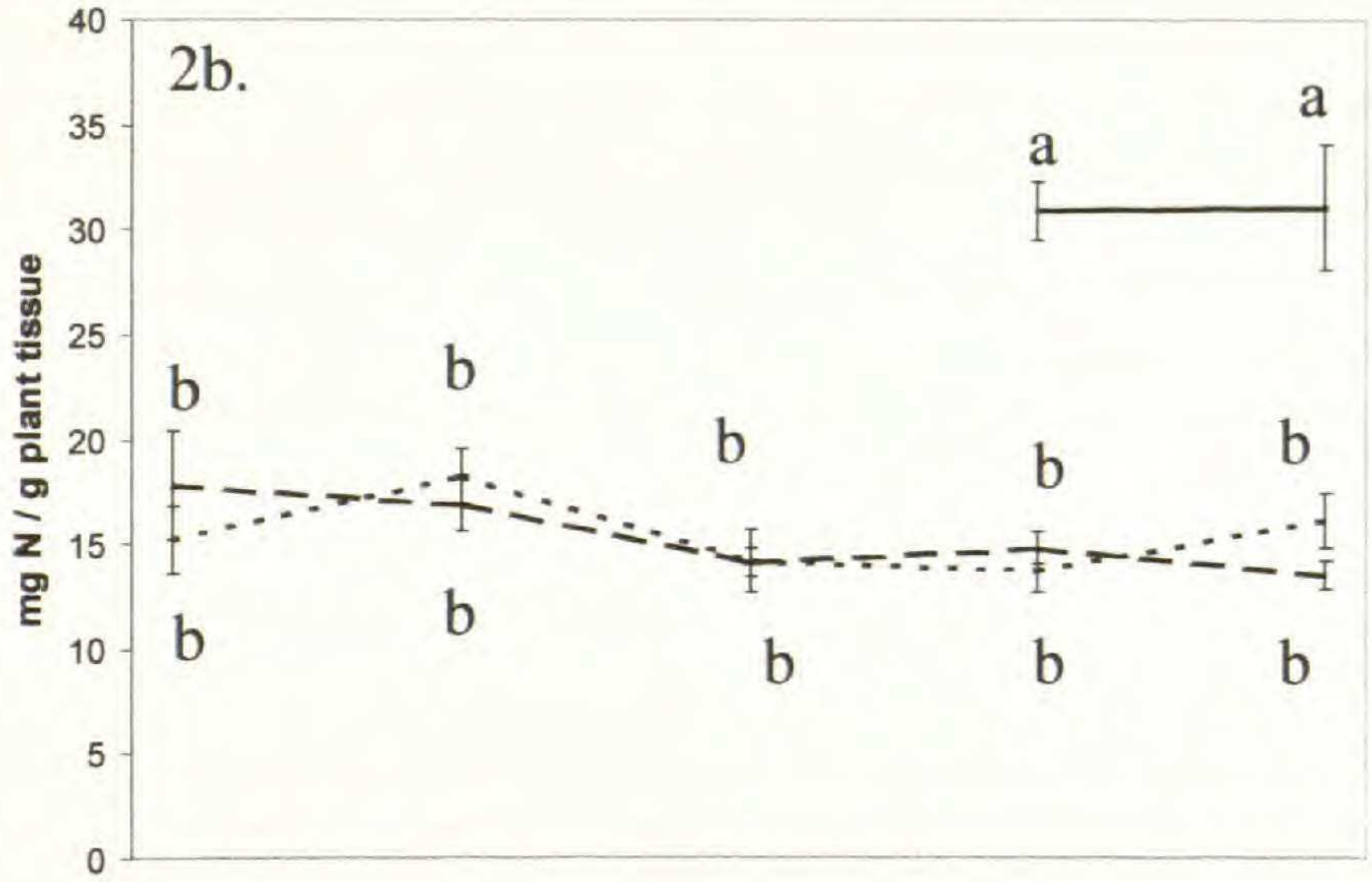
DISCUSSION

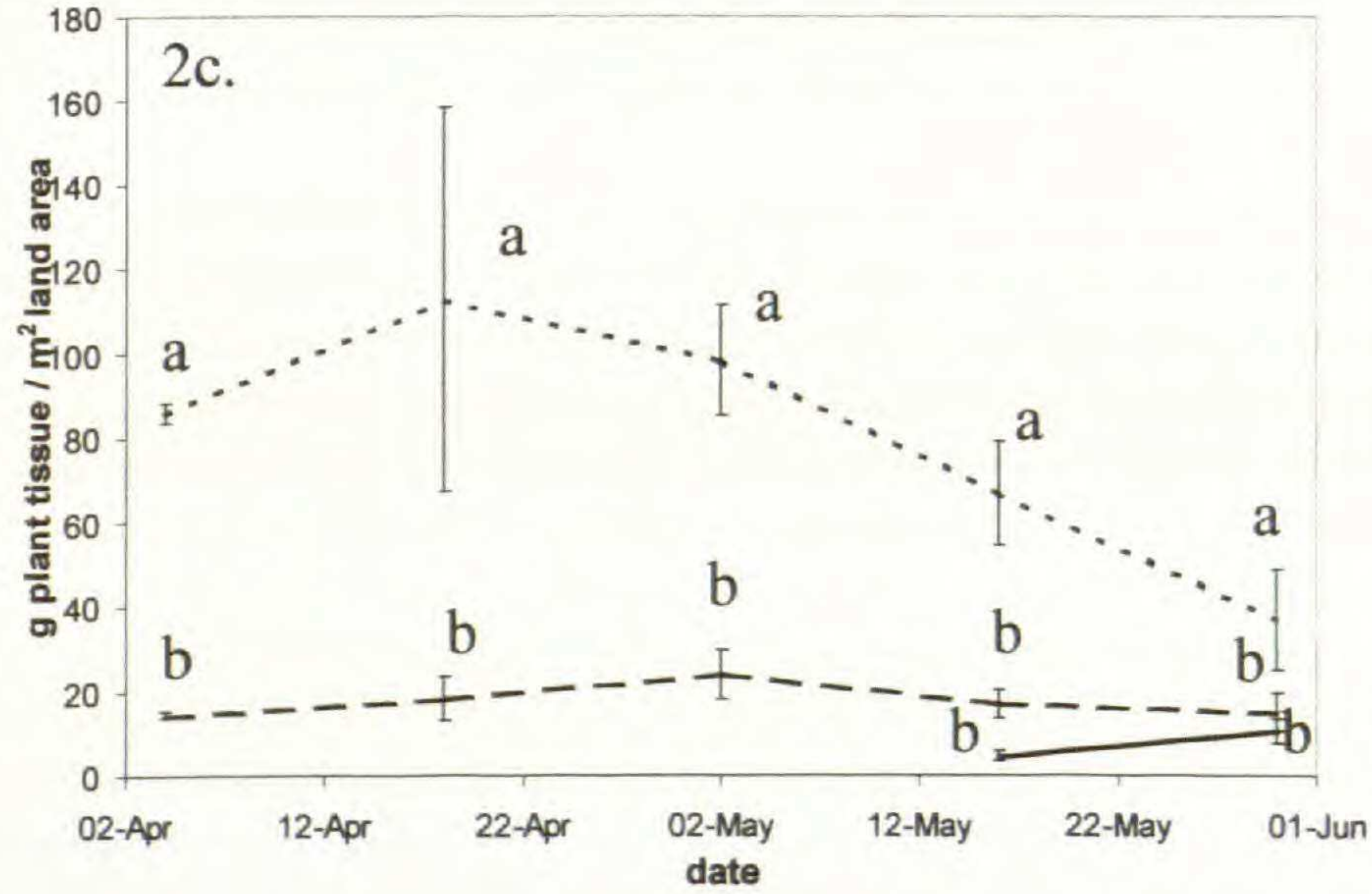
PHOTOSYNTHETIC RATE.–It is clear that the wintergreen fronds are photosynthesizing during spring. Rates observed in this study are comparable to autumn, winter, and spring rates in *Polystichum acrostichoides* (Minoletti and Boerner, 1993) and slightly higher than rates under experimental conditions in other shade-tolerant fern species (Ludlow and Wolf, 1975). Data for summer photosynthetic rates are unavailable for comparison. As the highest rates of

→

FIG. 2a. Nitrogen content of fern components through spring. 2b. Nitrogen concentration of fern components through spring. 2c. Biomass of fern components through spring. Means with the same letter were not significantly different at $\alpha = 0.05$. Errors bars indicate one standard error above and below the mean.


2a.
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
g N / m² land area
Old Fronds
New Fronds
Roots and Rhizomes
a
b
b
c
d
e
e
e
e
e
e
e


2b.
40
35
30
25
20
15
10
5
0
mg N / g plant tissue
a
a
b
b
b
b
b
b
b
b
b
b


2c.
180
160
140
120
100
80
60
40
20
0
g plant tissue / m² land area
02-Apr
12-Apr
22-Apr
02-May
12-May
22-May
01-Jun
date
a
a
a
a
a
b
b
b
b
b
b
b

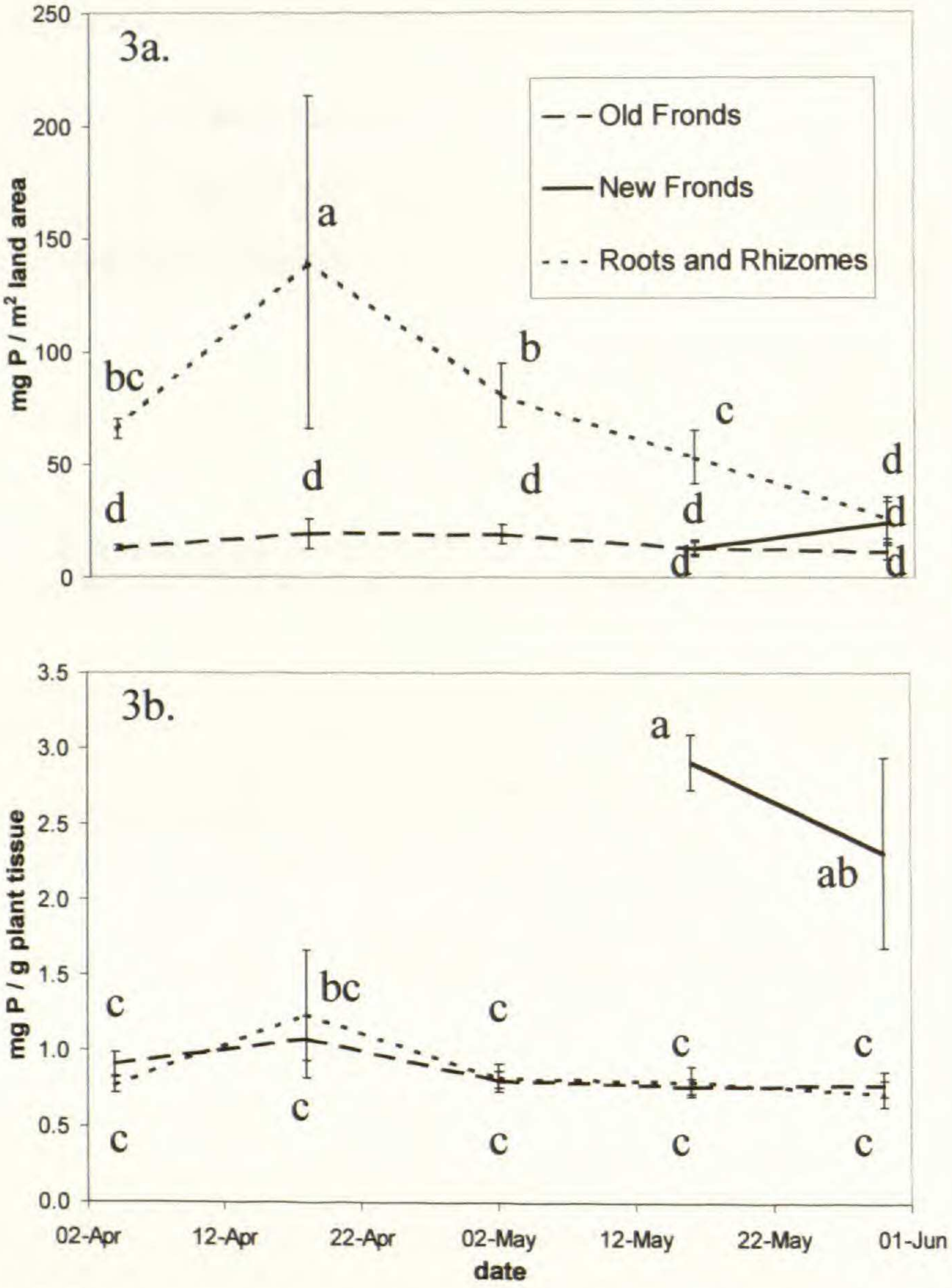


FIG. 3a. Phosphorus content of fern components through spring. 3b. Phosphorus concentration of fern components through spring. Means with the same letter were not significantly different at $\alpha = 0.05$. Error bars indicate one standard error above and below the mean.

net photosynthesis are observed early in the season (Figure 1), it is possible that photosynthesis may be occurring in these fronds during periods of the winter as well (Salisbury 1984, 1985), so long as light sufficiently penetrates the snow pack and temperatures permit metabolic activity.

The capacity to photosynthesize during spring may be important to annual net energy capture in *Dryopteris intermedia*. It may be critical to an understory species that usually receives low light levels in the shade of canopy species during the summer season (Anderson, 1964; Federer and Tanner, 1966; Hutchison and Matt, 1977) to take advantage of high light conditions prior to canopy leaf out. Spring ephemerals, species that develop above ground early in spring and senesce with canopy leaf out, are capable of high rates of photosynthesis during spring as compared to summer rates (Harvey 1980) and are adapted to growth and reproduction during this period of high light prior to canopy leaf out. Also, some disturbance-adapted species can acclimate to periods of high light (Brach et al., 1993) and increase their photosynthetic rate. Since *Dryopteris intermedia* does not respond to these periods of high light (Brach et al., 1993), maintaining year-round photosynthetic capacity may be critical to optimizing productivity. A comparison of spring and summer photosynthetic rates would be valuable to test this hypothesis.

It is not clear, however, that the C fixed by the wintergreen fronds is translocated to the new fronds or to any other part of the fern. Carbon gained during the spring period may be lost to soil microbes as the fronds decompose and not be of any immediate benefit to the plant. The non-significant pattern of increased belowground biomass in early spring (Figure 2c) suggests that carbon may be moving from the photosynthesizing fronds into the belowground tissue. A critical next step would be to conduct a tracer study to isolate the intermediate and eventual sinks for the spring-fixed carbon.

NITROGEN AND PHOSPHORUS POOLS.—As is typical for many herbaceous perennial plants (Zavitkovski, 1976), much more biomass is present belowground in *Dryopteris intermedia* than in aboveground components (Figure 2c). The mean root:shoot for biomass is roughly 4:1 through the spring. Unlike biomass, the concentration of N and P does not differ between mature parts of the plant. In fact the vernal constancy in N and P concentration and content in the wintergreen fronds suggests that no net mineral nutrient retranslocation to the rest of the plant is occurring with frond senescence. This contrasts with nutrient retranslocation patterns seen during senescence in other herbaceous understory plants (DeMars and Boerner, 1997). Short senescence times can result in greater retranslocation efficiency (del Arco et al., 1991). Slow senescence of the wintergreen fronds (from snowfall through mid spring) may preclude efficient retranslocation in this species. Therefore, maintaining wintergreen fronds as storage organs may not benefit the plant in the retranslocation and subsequent use of the nutrients.

PHOTOSYNTHETIC NUTRIENT USE EFFICIENCY.—Maintenance of the wintergreen fronds does, however, increase the nutrient retention time of N and P, thereby increasing nutrient use efficiency (Escudero et al., 1992) of these often limiting nutrients (Chapin, 1980; Vitousek and Howarth, 1991; Yanai, 1992). How much of an increase in nutrient use efficiency does the maintenance of wintergreen fronds in *Dryopteris intermedia* provide? Often nutrient use efficiency is defined as the inverse of the nutrient concentration (Vitousek, 1982; Shaver and Mellilo, 1984; Hirose and Werger, 1994; Minotta and Pinzauti, 1996; Fisk et al. 1998). This definition does not take into account energy expended for reproductive and maintenance efforts, only those expended for growth. Therefore, simply examining the inverse of the nutrient concentration may ignore significant uses of nutrients. A more useful assessment of nutrient use efficiency examines total carbon fixed per unit nutrient termed the Potential Photosynthetic Nutrient Use Efficiency (Field and Mooney, 1986; Hirose and Werger, 1994).

In this study, ambient light intensities were used to assess net photosynthetic rates since these rates are a better representation of the actual benefit of maintaining wintergreen fronds than would be light saturated net photosynthetic rates. Photosynthetic nutrient use efficiencies (PNUE) were 9.80, 1.44, and 2.96 μmols CO_2 / g / second for nitrogen on April 3, April 31, and May 14, respectively. For phosphorus PNUE were 0.19, 0.03, and 0.06 μmols CO_2 / mg / second on April 3, April 31, and May 14, respectively. Vitousek (1982) points out that one way to improve nutrient use efficiency is by fixing C for a longer period of time. In this case, springtime photosynthesis in wintergreen fronds clearly improves nutrient use efficiency since without this springtime photosynthesis PNUE would be zero until the new fronds began photosynthesizing.

In summary, vernal net photosynthesis does occur in the wintergreen fronds of *Dryopteris intermedia,* however it is not clear that the fixed carbon is translocated to the rest of the plant, and a tracer study would be useful to test this possibility. No evidence of N and P retranslocation from senescing wintergreen fronds to the rest of the fern plant was observed. Maintenance of wintergreen fronds may simply increase photosynthetic nutrient use efficiency of nitrogen and phosphorus. Future studies should examine the long-term fate of carbon and mineral nutrients held within senescing fronds and compare spring and summer photosynthetic rates in this species.

ACKNOWLEDGMENTS

Several people and organizations assisted with this work and the author thanks each of them for their assistance. The Frost Valley YMCA permitted use of their forested property and the New York City Department of Environmental Protection provided funding. Sam McNaughton permitted the use of his LCA-3. Lisa Tessier, Kim Anderson, Tim Schreiber, Karl Didier, Steve Fuller, Dave Kubek, Scott Jones, Kim Keirnan, and Tom Touchet assisted with work in the field. Don Bickelhaupt assisted with the Kjeldahl digestions and Marlene Braun and Deb Driscoll assisted with the ICP. Dudley Raynal, Scott Heckathorn, Ruth Yanai, and an anonymous reviewer commented on earlier versions of the manuscript and provided many helpful suggestions. Lastly, the SUNY College of Environmental Science and Forestry's Ecolunch group provided intellectual input and support.

LITERATURE CITED

ANALYTICAL DEVELOPMENT CO. LTD. 1988. *Instruction Manual Type LCA-3 Carbon Dioxide Leaf Chamber Analysis System.* Analytical Development Co. Ltd., Hoddesdon, England. 33pp.

ANDERSON, M. C. 1964. Studies of the woodland light climate II. Seasonal variation in the light regime. J. Ecol. 52:643–663.

AVERY, T. E. and H. E. BURKHART. 1994. *Forest Measurements.* 4th Edition. McGraw-Hill., New York. 408pp.

BICKELHAUPT, D. H. and E. H. WHITE. 1982. *Laboratory Manual for Soil and Plant Tissue Analysis.* State University of New York College of Environmental Science and Forestry. Syracuse, New York. 67pp.

BRACH, A. R., S. J. MCNAUGHTON, and D. J. RAYNAL. 1993. Photosynthetic adaptability of two fern species of a northern hardwood forest. Amer. Fern J. 83:47–53.

CHABOT, B. F. and D. J. HICKS. 1982. The ecology of leaf life spans. Ann. Rev. Ecol. Syst. 13:229–259.

Chapin III, F. S. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233–260.

Creed, I. F., L. E. Band, N. W. Foster, I. K. Morrison, J. A. Nicolson, R. S. Semkin, and D. S. Jeffries. 1996. Regulation of nitrate-N release from temperate forests: A test of the N flushing hypothesis. Water Resour. Res. 32:3337–3354.

del Arco, J. M., A. Escudero, and M. V. Garrido. 1991. Effects of site characteristics on nitrogen retranslocation from senescing leaves. Ecology 72:701–708.

DeMars, B. G. and R. E. J. Boerner. 1997. Foliar phosphorus and nitrogen resorption in three woodland herbs of contrasting phenology. Castanea 62:43–54.

Escudero, A., J. M. del Arco, I. C. Sanz, and J. Ayala. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. Oecologia 90:80–87.

Evans, J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78: 9–19.

Federer, C. A. and C. B. Tanner. 1966. Spectral distribution of light in the forest. Ecology 47: 555–560.

Field, C. and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. In: T. J. Givinish., ed., *On the Economy of Plant Form and Function*. Cambridge University Press. New York. 717pp.

Fisk, M. C., S. K. Schmidt, and T. R. Seastedt. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. Ecology 79:2253–2266.

Gilman, L. B. 1988. *General Guidelines for Microwave Sample Preparation*. CEM Corporation. Matthews, North Carolina.

Gildner, B. S. and D. W. Larson. 1992. Seasonal changes in photosynthesis in the desiccation-tolerant fern *Polypodium virginianum*. Oecologia 89:383–389.

Harvey, G. W. 1980. Seasonal alteration of photosynthetic unit sizes in three herb layer components of a deciduous forest community. Amer. J. Bot. 67:293–299.

Hirose, T. and M. J. A. Werger. 1994. Photosynthetic capacity and nitrogen partitioning among species in the canopy of a herbaceous plant community. Oecologia 100:203–212.

Hutchison, B. A. and D. R. Matt. 1977. The distribution of solar radiation within a deciduous forest. Ecol. Monogr. 47:185–207.

Lulow, C. J. and F. T. Wolf. 1975. Photosynthesis and respiration rates of ferns. Amer. Fern J. 65:43–48.

Mahall, B. E. and F. H. Bormann. 1978. A quantitative description of the vegetative phenology of herbs in a northern hardwood forest. Bot. Gaz. 139:467–481.

Minoletti, M. L. and R. E. J. Boerner. 1993. Seasonal photosynthesis, nitrogen and phosphorus dynamics and resorption in the wintergreen fern *Polystichum acrostichoides* (Michx.) Schott. Bull. Torrey Bot. Club 120:397–404.

Minotta, G. and S. Pinzauti. 1996. Effects of light and soil fertility on growth, leaf chlorophyll content and nutrient use efficiency of beech (*Fagus sylvatica* L.) seedlings. Forest Ecol. Managem. 86:61–71.

Mitchell, M. J., D. J. Raynal, and C. T. Driscoll. 1996. Biogeochemistry of a forested watershed in the central Adirondack Mountains: Temporal changes and mass balances. Water, Air, and Soil Pollution 88:355–369.

Monk, C. D. 1966. An ecological significance of evergreenness. Ecology 47:504–505.

Moore, P. D. 1984. Why be an evergreen? Nature 312:703.

Murdoch, P. S. and J. L. Stoddard. 1992. The role of nitrate in the acidification of streams in the Catskill Mountains of New York. Water Resour. Res. 28:2707–2720.

Murdoch, P. S. and J. L. Stoddard. 1993. Chemical characteristics and temporal trends in eight streams of the Catskill Mountains, New York. Water, Air, and Soil Pollution 67:3667–395.

Reifsnyder, W. E., G. M. Furnival, and J. L. Horowitz. 1971. Spatial and temporal distribution of solar radiation beneath forest canopies. Agricultural Meteorology 9:21–37.

SAS Institute Inc. 1997. Selected SAS Documentation for APM 620: Analysis of Variance (Spring 1998). SAS Institute Inc. Cary, North Carolina.

Salisbury, F. B. 1984. Light condition s and plant growth under snow. In: J. F. Merritt, ed., *Winter Ecology of Small Mammals*. Carnegie Museum of Natural History. Pittsburgh. 380pp.

———. 1985. Plant growth under snow. Aquilo, Ser. Bot. 23:1–7.

SHAVER, G. R. and J. M. MELLILO. 1984. Nutrient budgets of marsh plants: Efficiency concepts and relation to availability. Ecology 65:1491–1510.

VAN BUSKIRK, J. and J. EDWARDS. 1995. Contribution of wintergreen leaves to early spring growth in the wood fern *Dryopteris intermedia*. Amer. Fern J. 85:54–57.

VITOUSEK, P. M. 1982. Nutrient cycling and nutrient use efficiency. Amer. Naturalist 119:553–572.

VITOUSEK, P. M. and R. W. HOWARTH. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochem. 13:87–115.

YANAI, R. D. 1992. Phosphorus budget of a 70-year-old northern hardwood forest. Biogeochem. 17:1–22.

ZAVITKOVSKI, J. 1976. Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. Ecology 57:694–706.

ZHANG, Y. and M. J. MITCHELL. 1995. Phosphorus cycling in a hardwood forest in the Adirondack Mountains, New York. Canad. J. Forest. Res. 25:81–87.